

ECOTYPIC VARIATION OF THE PHOTOPERIODIC RESPONSE IN POPULUS

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With eight text-figures

INTRODUCTION

DURING THE PAST FEW DECADES, the traditional and complacent notion that genetic differences within tree species are nonexistent or negligible has been gradually discarded. Most silviculturists are no longer content with the assumption that diversity within tree species can be adequately explained in terms of environment alone. Such a fundamental revision in biological theory has, quite naturally, produced a marked impact on silvical research methods and silvicultural practice.

The limitations, for example, of the descriptive method as a means of analyzing intraspecific diversity have become increasingly apparent. Although field observation and description of phenotypes and environment provide useful and essential preliminary data for the analysis of observed diversity, the method provides no means for determining the relative amounts of environmental fluctuation and genetic variation involved.

The solution of such silvical problems is, however, possible by transplant methods that have been perfected by various workers (Turesson, 19; Turrill, 20; Clausen, Keck and Heisey, 2; and others). One application involves the transplantation of different genetic types into a uniform environment. Under such conditions the effects of differences in habitat on the phenotype are eliminated, and the genotypes of different individuals of the group under investigation may be compared directly. For information on the rigidity or plasticity of genotypes, wild representatives of the species may be propagated vegetatively, and the clonal lines thus established may be planted under different environmental conditions. Both methods have been used in the photoperiodic studies here reported, and form one of the approaches to silvical problems currently under investigation by the Cabot Foundation.

Source of Material

Initial sampling of wild populations in *Populus* species native to North America was begun in the fall and winter of 1947-48, and has been continued annually since that time. During the period 1947-50 principal emphasis was placed on obtaining representatives of *P. trichocarpa* (western balsam poplar or so-called "northern black cottonwood"), native of the

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Pacific coast region, and the *P. deltoides* complex (eastern cottonwood) of the eastern United States. These collections were all in the form of branch or stem cuttings taken from what were determined to be average, healthy specimens growing under natural conditions at the various collection points. The use of cuttings was designed to insure that the clonal lines represented were derived from individuals known to be capable of survival in their native habitat. Since species in the section TACAMAHACA (balsam poplars) are uniformly good rooters from plants of any age, there was no need to restrict selected individuals of *P. trichocarpa* to the younger age classes. On the other hand, because of the poor rootability of cuttings from old trees, almost all of the *P. deltoides* clonal lines established were started from cuttings taken from plants 2 to 6 years of age.

The photoperiodic studies here reported are primarily concerned with clones of *P. trichocarpa* and the *P. deltoides* complex collected during the period 1947–50; but reference is also made to clonal line collections of *P. tacamahaca* (balsam poplar) made during the same period, and to collections of various other *Populus* species acquired in the spring of 1950 and subsequently.

Approximate ranges of *P. trichocarpa* and *P. deltoides* and the locality of origin for the various clonal lines of these species used in the photoperiodic studies are shown in FIGURE 1.

Although a portion of the field collection was done by the senior author, the bulk of the material was made available through the generous assistance and cooperation provided by numerous state and federal forestry agencies in the United States, and similar provincial and dominion organizations in Canada. Especially extensive contributions have been made by the U. S. Forest Service, U. S. Soil Conservation Service, Dominion Forest Service, and many state and provincial conservation departments within the ranges of the species concerned.

Experimental Areas

The principal propagation and test plantation site utilized by the Cabot Foundation is located in the town of Weston, Middlesex County, Massachusetts, about 10 miles west of Boston. The area is part of the former Case Estate, given to the Arnold Arboretum about a decade ago. The portion of several acres which has been allocated to the Cabot Foundation was formerly used as a pasture or mowing. The soil is, in general, uniform and the surface flat. The elevation is 200 feet, and lies somewhat lower than most of the surrounding area. For this reason temperature inversions in early fall may result in a somewhat shorter frost-free season than the average of 148 days for the Weston area as based on records of the Weston Weather Bureau Station (located ca. 2 miles northwest of the Case Estate at an elevation of 224 feet).

A portion of the Weston tract has been devoted to the propagation of the clonal lines assembled since the 1947–48 season, while the remainder of the area has been set aside for the establishment of permanent test plantations.

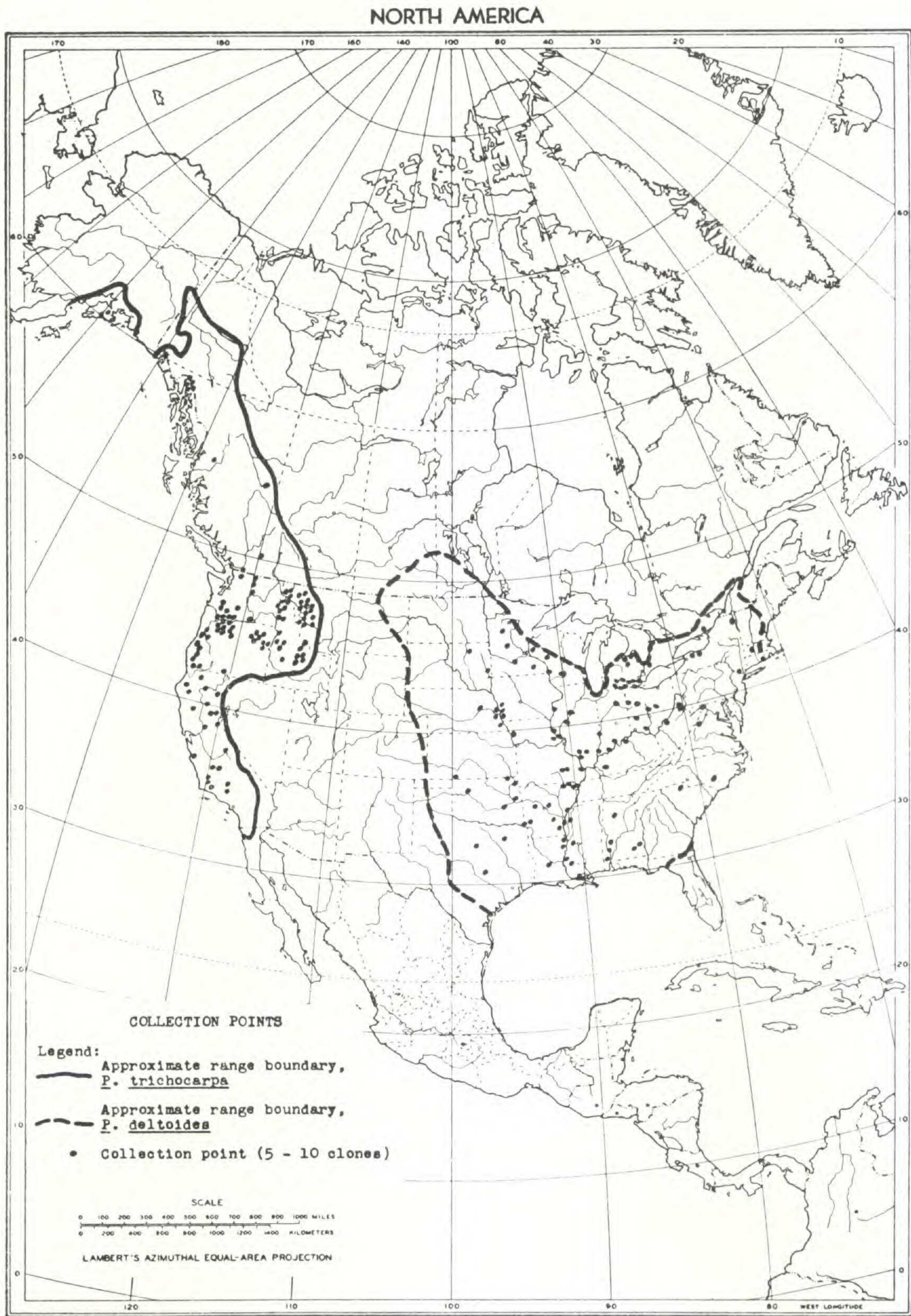


FIG. 1. Approximate ranges of *P. trichocarpa* and *P. deltoides* and collection points for clones used in this study.

Although two such plantations were established in 1950 and 1951, observations at Weston on the date of cessation of height growth for the various clones concerned in this study were all made in the propagation area, hereafter referred to simply as the "Weston area."

The combined experimental facilities of the Arnold Arboretum and the Bussey Institution, located in Jamaica Plain, Massachusetts, a part of greater Boston (ca. 10 miles southeast of Weston), have also been used in this study. The outdoor long-day and normal-day plots used in the 1951 experiments were set out in a portion of the experimental plots used jointly by these institutions, and located on a flat gravelly knoll in the first range of hills south of the Boston basin. The soil, thanks to continuous enrichment and good management, is highly fertile and uniform.

PHOTOPERIODIC RESPONSES IN PLANTS

Biologists, as well as most primitive peoples, have long recognized the indispensable nature of solar energy in the biological scheme. But only within the past thirty years have botanists recognized the notable significance to plant growth and development that is associated with the periodic manner in which this energy is supplied to the earth's surface.

Within the tropical and subtropical regions of the world, there is little change in the length of the daylight period throughout the year; but outside these regions, marked seasonal differences occur. At the latitude of Boston (ca. 42° N.), for example, the length of the daylight period on the shortest day of the year is ca. 9 hours, and on the longest day ca. 15 hours, i.e., a difference of 6 hours (FIG. 2). With increases in latitude the annual variation in day-length is greater. Thus, at the latitude of Juneau, Alaska (ca. 58° N.), day length at the time of the winter solstice is ca. 6.5 hours as compared with ca. 18.5 hours on the day of the summer solstice, a difference of 12 hours. The above day lengths are based on the time of sunrise and sunset. Actually, the effective photoperiods at all latitudes are somewhat greater due to the effects of the morning and evening twilight periods (Fig. 2).

Flowering Response

The response in growth and development exhibited by plants in relation to the length of the daily light period (i.e., *photoperiod*) is called *photoperiodism*. The earlier and, indeed, most of the later investigations concerned with this phenomenon have centered on the flowering response of various herbaceous plant species and varieties when exposed to photoperiods of varying length.

First recognition of the influence of day length on reproductive development in plants was made by Garner and Allard (3) in 1920. These workers observed that Maryland Mammoth tobacco, which normally does not flower in the field during the summer season at the latitude of Washington, D. C. did, nevertheless, flower profusely when grown in a green-

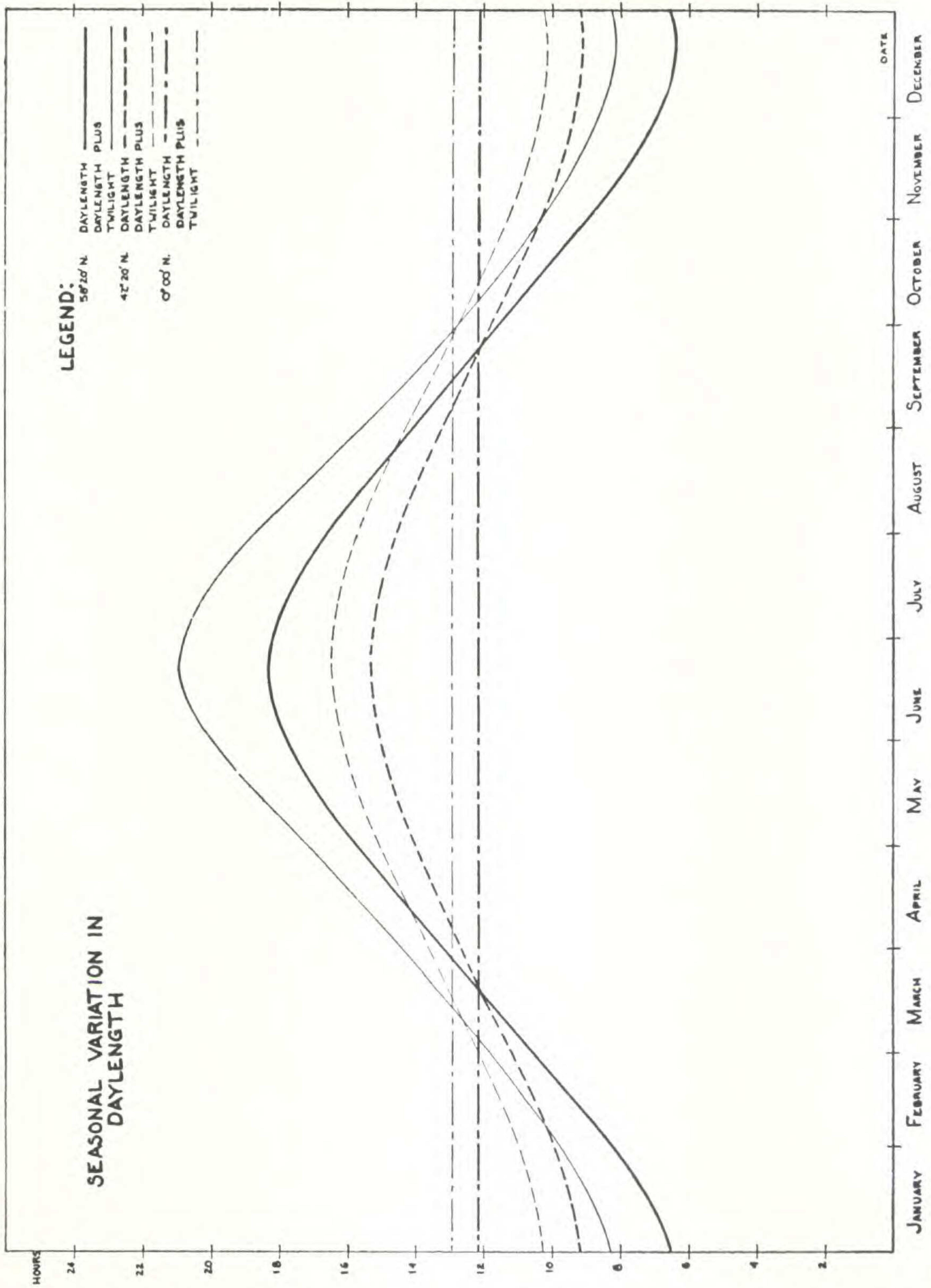


FIG. 2. Seasonal variation in day length at various latitudes: equator, 42° 20' N. and 58° 20' N.

house at the same latitude during the winter. The dissimilar reproductive development observed led to the hypothesis that day length was a controlling environmental factor, the relatively short photoperiods of winter apparently favoring flower production in this variety. Subsequent confirmation of this hypothesis was made through the use of carefully controlled experiments by these and numerous other workers.

The significance of the photoperiodic influence on flowering is obviously a matter of much practical concern in the case of cultivated crops grown for their fruit or seeds. Many of the grains, for example, require long days to flower, and for this reason long-day varieties cannot be successfully moved to southern latitudes. Other long-day plants grown for the food stored in their vegetative organs, such as spinach, lettuce, and radish, must be grown as spring or autumn crops in regions where the long days of summer would otherwise cause them to "bolt."

In order for such short-day plants as the Biloxi soy bean and numerous ornamentals (cosmos, aster, chrysanthemum, etc.) to flower, they must be grown either in the low latitudes or in the short days of spring or autumn in the higher latitudes. Many short-day ornamentals native of the tropics are, of course, grown successfully in greenhouses under the short-day regime of the winter months in northern latitudes.

Plants indeterminate with respect to their photoperiodic requirements for flowering, such as tomato, cotton, buckwheat, and sunflower, may be grown successfully over a wide range of latitudes.

Vegetative Response

Although major interest in the photoperiodic studies involving herbaceous plants has centered on the influence of day length upon reproductive development, most workers have also noted marked effects on vegetative growth as well. Most plants exhibit much better vegetative development when exposed to long photoperiods than to short ones, regardless of the fact that they may be classified as "short-" or "long-day" types with respect to flowering. Maryland Mammoth tobacco, for example, when grown under the long days of summer at the latitude of Washington, D. C., by Garner and Allard (3), attained heights of 10–15 feet; whereas, when greenhouse grown in the short days of winter, it did not exceed five feet.

Conversely, movement of long- or short-day flowering types into natural or artificially created shorter days usually results in marked reduction in vegetative development.

Photoperiodic studies of woody plants have for the most part involved seedlings, and consequently little is known of the influence of day length on reproductiveness. These investigations have, however, demonstrated that variation in day length is a factor of marked importance in the annual vegetative growth cycle of many woody species, particularly as it relates to the control exerted over the timing of physiological processes concerned in the onset of dormancy.

In common with techniques used in the investigation of photoperiodic

responses in herbs, studies of woody plants have involved the testing of various species in a day-length regime different from that prevailing in their native habitat. Whether such tests have involved actual movement of the plants north or south into a new natural day-length pattern, or if short or long days have been artificially created at any particular latitude, the results have been the same. In general, movement from the latitude of the natural habitat northward (i.e., into longer days) prolongs the active period of growth; and movement southward (i.e., into shorter days) shortens it. Such modifications in the length of the active growth period normally result in marked differences in total seasonal increment and frost hardiness. Thus, movement of plants into a day-length regime longer than that of the native habitat characteristically gives increased height growth accompanied by decreased resistance to early autumnal frosts; whereas movement into a short-day regime results in dwarfing, associated with increased frost resistance.

Similar photoperiodic growth responses have been, with but few exceptions, demonstrated by Moshkov (12, 13, 14) and Bogdanov (1) to characterize the behavior of various species in the following genera: *Acer*, *Aesculus*, *Ailanthus*, *Alnus*, *Caragana*, *Corylus*, *Fraxinus*, *Juglans*, *Larix*, *Phellodendron*, *Pinus*, *Prunus*, *Rhus*, *Robinia*, and *Ulmus*; by Kramer (8) and Jester and Kramer (6) in North American species of the following genera: *Acer*, *Fraxinus*, *Fagus*, *Robinia*, *Liriodendron*, *Liquidambar*, *Quercus*, and *Pinus*; by Sylvén (18) in the European aspen (*P. tremula*); by Johnsson (7) in *Betula*; by Langlet (9) in Scotch pine; and by Olmsted (15) in sugar maple.

INFLUENCE OF PHOTOPERIOD ON TIME OF HEIGHT GROWTH CESSATION IN *POPULUS*

First suggestions of photoperiodic sensitivity among the clones in the propagation area at Weston appeared during the first (1948) growing season. As a result of early height growth cessation and consequent dwarfing, *P. trichocarpa* ecotypes from high latitudes stood out in sharp contrast to those of more southerly origin.

Interclonal Responses to a Uniform Day Length

Precise measurements of height increment by the use of auxanometers of various design have been made by several workers. By their use the time of terminal growth cessation could doubtless be pinned down to a certain hour, or at least to a particular day. Such methods are not, however, practical for the measurement of large numbers of individuals in the field, since the cost would be prohibitive.

In the present studies total height measurements were taken to the nearest centimeter at 7-day, 5-day or 3-day intervals by direct measurement with meter sticks or tapes. Although lacking a high degree of precision, the technique is sufficiently accurate for determining comparative

differences in growth cessation which are spread over a period of several weeks or months. The error occurs during the period immediately preceding the time of actual height growth cessation. The increments between measurements during this period may be so small that the actual day of growth cessation is indeterminable. Depending upon the interval between measurements and other variables, deviations in the date of recorded growth cessation probably vary in the order of 3 to 7 days before and after the actual date of growth cessation. In general this method tends to encourage a later recording of growth cessation.

First systematic recording of the time of height growth cessation in the *Populus* collections was made during the 1950 season in the propagation area at Weston. Relatively small samples of *tacamahaca* and *deltoides* clones were included in the study, the majority being *trichocarpa*. All were derived from cuttings which had been planted in the spring of 1948 or 1949 and were thus in their second or third growing season. Measurements of total height for each of the clones included in the study were taken at weekly intervals from June 27 to November 7.

Active terminal growth in the group of *tacamahaca* clones measured was observed to occur over a period of about 158 days (April 14 to September 19); in the *deltoides* clones over a period of about 178 days (April 20 to October 15); and in the *trichocarpa* group over a period of about 197 days (April 14 to October 28). Although the first killing frost of autumn at Weston occurred the night of September 24–25, the growing season was by no means ended. Plants still in active height growth at that time (*deltoides* and *trichocarpa* of southern origin) suffered some damage to the young unfolding leaves near the growing point, but continued in active height growth thereafter. Subsequent light frosts in October (on the 6th, 8th, 16th, and 21st) caused similar damage; but height growth persisted in some clones until the first heavy frosts of October 26 and 27. These frosts were apparently of sufficient severity to kill all meristematic tissue in the growing points of the plants still active at that time.

The recorded dates of height growth cessation for the various *tacamahaca* clonal lines ranged from about June 20¹ to September 19, a period of 91 days, representing 58 percent of the growing season. Among the *deltoides* group, cessation of height growth occurred between August 15 and October 18, a period of 64 days, or 31 percent of the growing season. The time of height growth cessation in the *trichocarpa* clones was considerably more widespread: first terminal growth cessation was recorded about June 20,¹ and the last on October 28, a period of 130 days, or about two-thirds of the growing season.

Since this considerable intraspecific diversity in time of terminal growth cessation occurred under the essentially uniform environment prevailing in the propagation area at Weston, the conclusion is inevitable that the vari-

¹ Measurements were started on June 27. This date proved too late to record the cessation of height growth of certain *tacamahaca* and *trichocarpa* clones of high latitude origin. Subsequent observations in 1951, 1952, and 1953 have confirmed that height growth in these clones stops ca. June 20.

ous clones within the species observed are genetically diverse in this character. That this diversity is not randomly distributed throughout the range of each species, but is inversely correlated with latitudinal distribution, is revealed by the scatter diagrams that result when latitude of origin for each clone of each species is plotted over the corresponding date on which height growth ceased at Weston (Figs. 3, 4 and 5). The correlation coefficients for these diagrams are all high ($r = -.893$, $-.706$, and $-.823$ respectively), and all exceed the 1 percent level of significance.

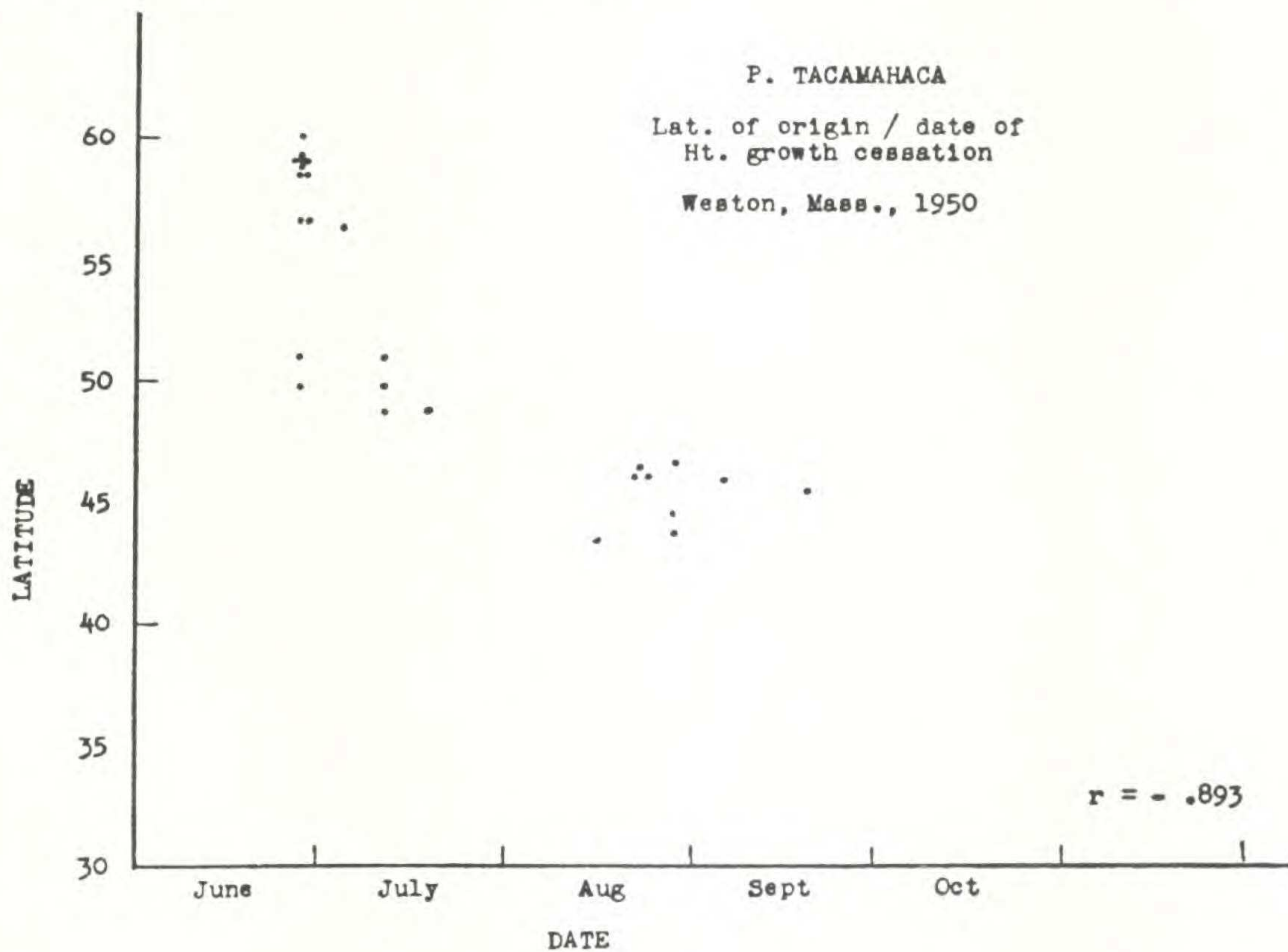


FIG. 3.

The trend of the gradient revealed by these diagrams clearly indicates a tendency for clones of high latitude (long-day) origin to cease terminal growth early, and clones of low latitude (short-day) origin to stop terminal growth late when grown under the mid-latitude day-length regime prevailing at Weston. These results are in agreement with the photoperiodic growth reactions which characterize the behavior of European aspen (Sylvén, 18) and species in other genera when subjected to day-length regimes differing from those in their native habitats. As previously pointed out, various workers have demonstrated that the movement of plants from native habitats of long day into short day is normally characterized by earlier height growth cessation; whereas movement from short day into long day results in delayed growth cessation. As a working hypothesis it therefore appears tenable to conclude that the inverse correlation between latitude of origin and time of terminal growth cessation for the ecotypes

of the *Populus* species here concerned is the result of similar photoperiodic reactions between the various genotypes of the ecotypes represented and the uniform day-length regime to which each was exposed at Weston.

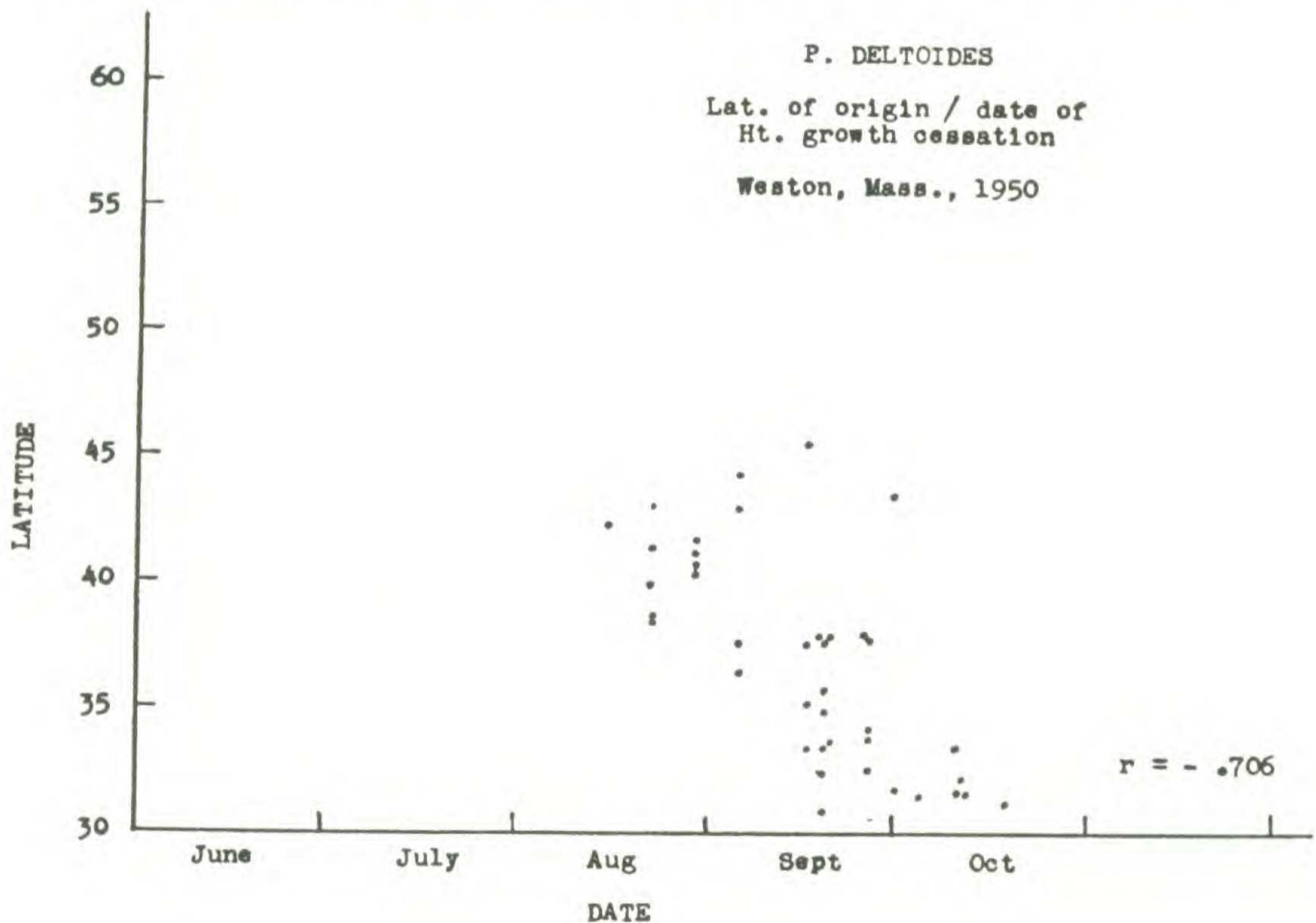


FIG. 4.

Although the clinal nature of the variation is sufficiently well-defined in these diagrams to support the above hypothesis, there is ample evidence to suggest that the relationship between time of height growth cessation at Weston and latitude of origin of the various clones is not necessarily simple and direct. The spread in dates of growth cessation from mid-July to late October among the *trichocarpa* clones native of latitudes between 40° and 50° (FIG. 5), for example, indicates that a pronounced local diversity in photoperiodic response exists, apparently quite independent of latitudinal origin.

That diversity in photoperiodic response may occur locally within a species population under essentially uniform day-length conditions leads to interesting speculation. There can be little doubt, in the first place, that height growth cessation in *Populus* signals the onset of initial physiological processes culminating in winter dormancy. The time during the growing season at which terminal growth cessation occurs thus assumes a role of critical survival value. Through the selective pressure exerted by the first killing frosts of autumn, only those genotypes capable of terminating height growth at a sufficiently early date to escape such frosts are capable of survival. Within any uniform day-length zone, therefore, where the growing season varies considerably in length, due to topography or other factors, the hypothesis may be made that adaptation to any particular

length of growing season is effected through the selection of those genotypes having a suitable photoperiodic response to the prevailing day-length regime of that latitude.

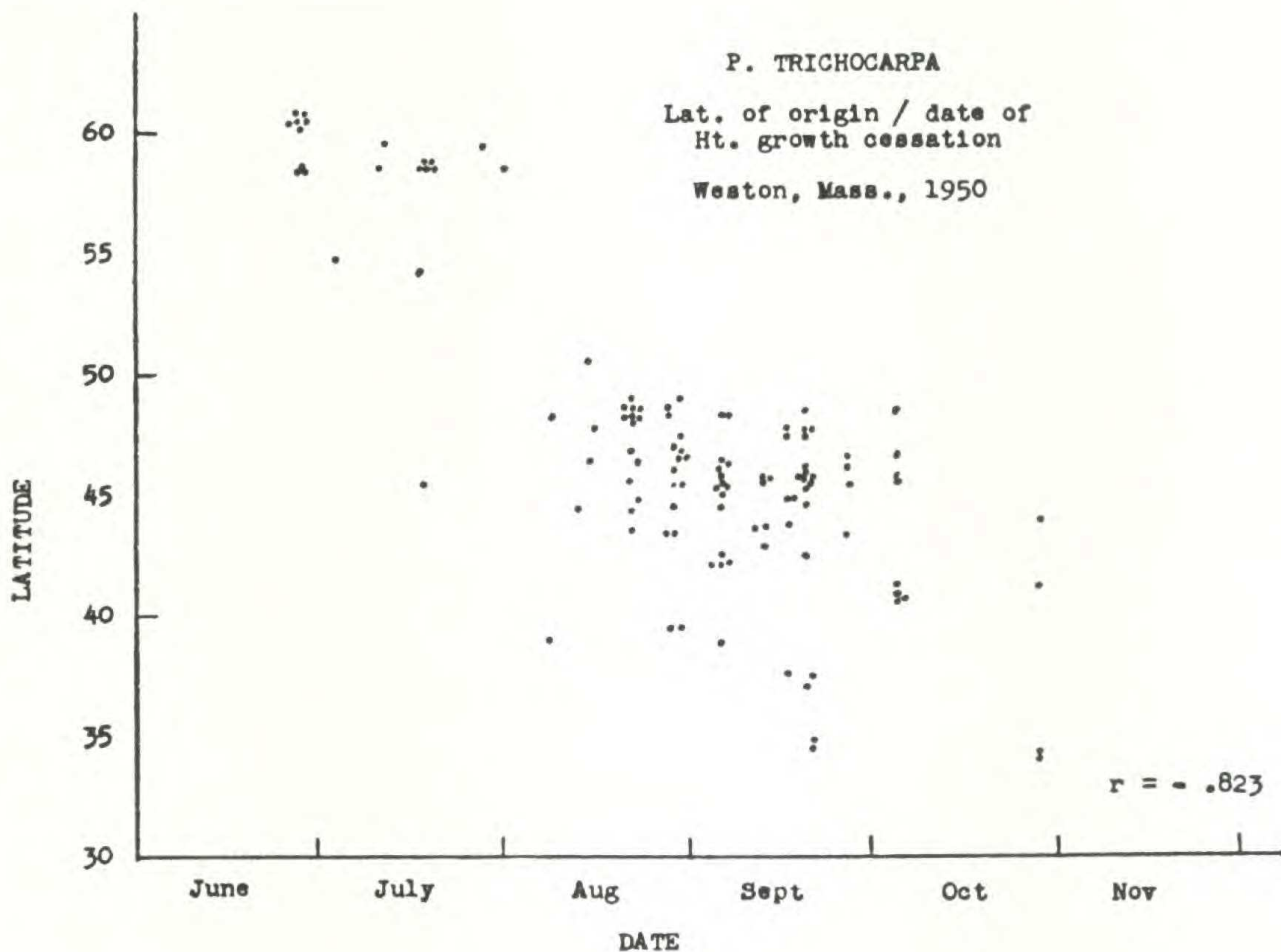


FIG. 5.

The group of clones originating between 40° and 50° (FIG. 5), referred to above, represents a case in point. This group is actually composed of a broad longitudinal sampling of *trichocarpa* ecotypes, extending from the Pacific coast to western Montana, and with a vertical dispersion from near sea level to ca. 5000 feet elevation. Since the length of the frost-free season in this latitudinal zone is, in fact, known to vary widely within comparatively short distances, due to elevation, the nature of the topography, etc., the considerable diversity in time of height growth cessation for clones native of the zone might be satisfactorily explained on the basis of the above hypothesis.

A direct test of the hypothesis may, of course, be made by determining the degree of correlation, if any, that may exist between the lengths of the growing season at the points of origin for clones native of a narrower latitudinal band (i.e., having an essentially uniform seasonal day-length regime) and the dates of height growth cessation for the same clones as recorded at Weston.

Although precise data on the average length of the growing season for the native habitats of each of the clones represented in our collections is for obvious reasons unavailable, reliable estimates nevertheless can be

made for those native to areas in the vicinity of U.S. Weather Bureau Stations (21).

FIGURE 6 shows the scatter diagram resulting when the length of the average growing season for those clones native only of the 2° latitudinal zone (45° to 47°) is plotted over the date of height growth cessation at Weston. The regression path here defined appears sufficiently uniform in trend ($r = +.789^1$) to confirm further the hypothesis that *trichocarpa* populations are capable of adaptation to growing seasons of varying length within uniform day-length zones by selection of those types having a suitable photoperiodic response.

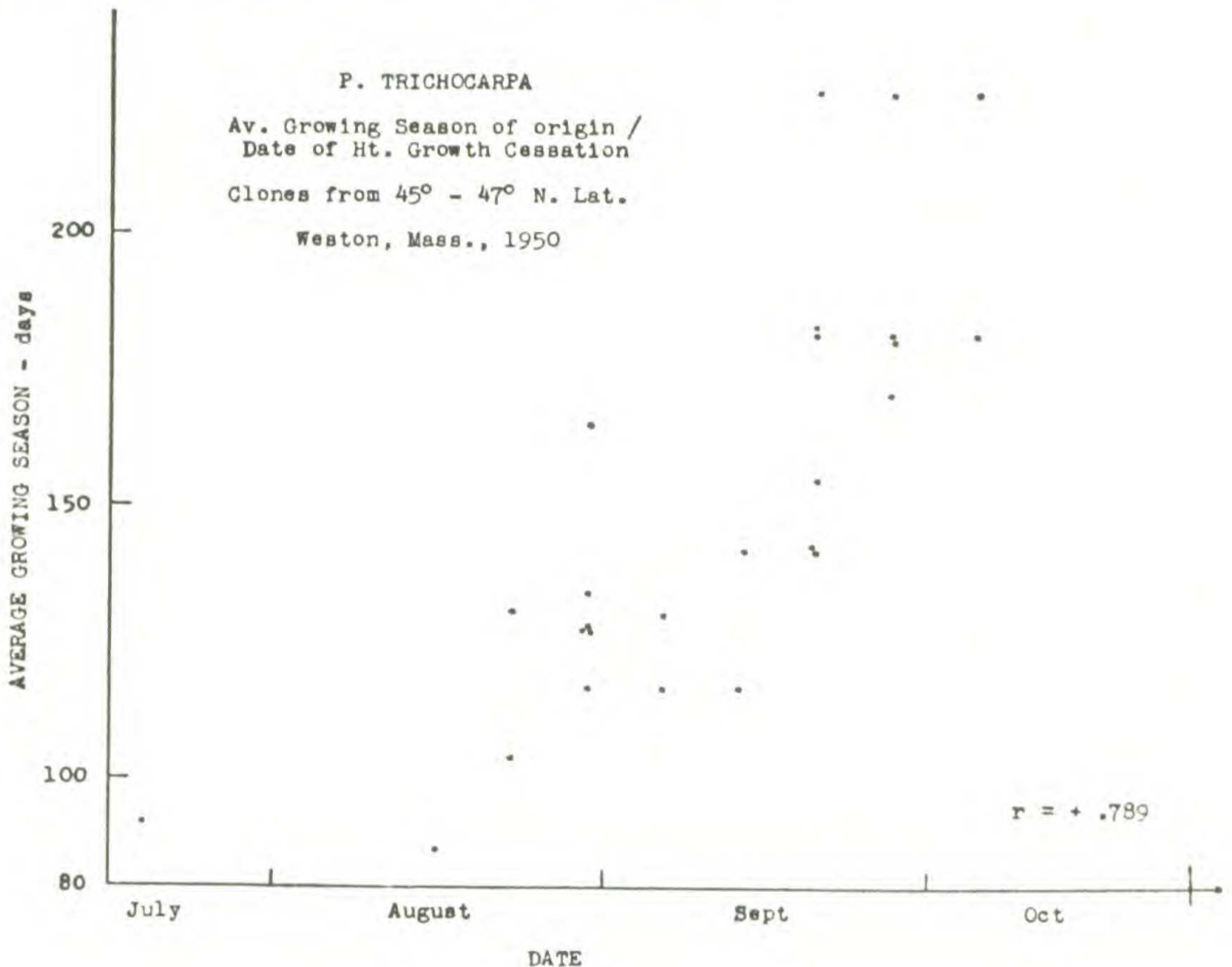


FIG. 6.

Intraclonal Responses to Diverse Day-length Patterns

During the 1950 and 1951 seasons, tests of photoperiodic sensitivity as revealed by influence on time of height growth cessation were made in about 100 clonal lines within the following species: *P. trichocarpa*, *P. tacamahaca*, *P. angustifolia*, *P. deltoides*, and various hybrids of *P. tremuloides* × *P. tremula*. The tests of 1950 were made in a greenhouse at the Arnold Arboretum with potted propagules of 45 clonal lines grown under short-, normal- and long-day photoperiods. Results of these observations have been previously published (Hoffmann, 4).

¹ Exceeds the 1 percent level of significance.

Similar tests of the same clonal lines, and about 55 additional, were made outside during the 1951 season in portions of the Bussey Institution nursery. Ramets of the various clones in these studies were exposed only to the natural-day pattern prevailing at the latitude of Boston (ca. $42^{\circ} 20'$ N.) and a long-day regime corresponding to that at Juneau, Alaska (ca. $58^{\circ} 20'$ N.).

Flood lights and reflectors for the long-day plot were so arranged as to obtain complete coverage of the area with a minimum ground surface light intensity of 1.5 foot candles. Since the work of Withrow and Benedict (22), Matzke (10), and others demonstrates that light intensities of less than 1 foot candle are capable of producing photoperiodic responses, twice the duration of civil twilight was added to the "sunrise to sunset" day length (FIG. 2). According to Humphreys (5), light intensity at the beginning of civil twilight (morning sun 6° below the horizon) is 0.4 foot candle with a clear sky, and quickly rises above 1 foot candle.

Supplemental light was supplied the long-day plot by means of an automatic time switch in the morning and evening. Adjustment of the switch settings was made every third day to conform to the natural day at Juneau. Use of the lights was discontinued on September 30, when the photoperiod of Boston became greater than that of Juneau. Thereafter both experimental plots received the normal day length of Boston.

The variable responses in terms of height growth cessation to different day-length regimes that were observed added further confirmation of the presumed photoperiodic sensitivity in *Populus*, and also demonstrated the apparent similarity of this response to that exhibited by other tree genera of the temperate zone.

Detailed tabulation of the data recorded in these studies cannot, in the interest of brevity, be included in the present paper. However, a sample of the records on height growth cessation for *P. trichocarpa* clones of various origins when grown under the normal Boston-day and the artificial long-day regimes at the Arnold Arboretum during the 1951 season are shown in TABLE 1 (Columns 7 and 8). Differences in time of growth cessation are noted in Column 9. Included also are recorded dates of height growth cessation of the same clones under normal-day conditions at Weston in 1950 and 1951 (Columns 5 and 6).

As these data indicate, diversity of intra-clonal response to normal- and long-day regimes was most pronounced in those clones (981 and 984) from high latitude habitats. The net phenotypic disparity in height and leaf development between ramets of such northern clones when grown in the long-day regime to which they are adapted and the shorter-day regime of Boston is most striking (FIG. 7).

Similarly, marked intra-clonal differences in time of height growth cessation characterize those clones adapted to the high-elevation (short growing season) habitats in the lower latitudes when grown in the normal- and long-day regimes (clones 1047, 1485, and 1239, TABLE 1). In contrast, intraclonal diversity in response to normal- and long-day photoperiods demonstrated by those clones originating in the low-elevation (long grow-

ing season) habitats of the lower latitudes is characteristically small (clones 895, 899, 825, and 957, TABLE 1).

TABLE 1
TIME OF HEIGHT GROWTH CESSATION IN NORMAL- AND LONG-DAY REGIMES
P. trichocarpa

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
Clone No.	Origin			Date of Ht. Growth Cessation				Difference (days) (8)-(7)
	Lat. (N)	Long. (W.)	Elev. (Ft.)	Normal Day		Long Day		
				Weston		Arn. Arb.		
				1950	1951	1951	1951	
981	60-37	149-30	1300		6/25	6/20	8/28	69
984	60-19	149-21	 ¹	6/19	6/20	8/19	60
1147	48-30	115-55	1850	8/29	8/28	8/28	10/3	36
1151	48-25	114-30	2100	8/29	8/28	9/12	9/27	15
1565	48-10	114-10	8000	8/1	7/31	8/28	9/27	30
1029	47-30	123-55	250	9/19		9/21	10/5	14
1047	47-35	115-25	2400	9/12		8/29	9/28	30
895	46-10	122-55	30	9/26	9/18	10/3	10/12	9
1485	46-20	112-15	5000	8/15	8/7	8/10	9/13	34
899	45-35	122-35	25	9/26	9/18	10/7	10/12	5
1324	45-15	117-45	3400	9/5	8/28	9/18	10/3	15
825	44-30	123-25	200	9/19	9/18	10/5	10/11	6
1239	44-30	114-15	5200	8/29	8/28	8/31	10/3	33
957	43-25	123-25	500	9/26	9/18	10/6	10/11	5
1137	43-35	114-25	5300	8/29	8/28	8/31	9/27	27

¹ Height growth cessation occurred prior to June 27, 1950.

A point of considerable physiological interest is suggested by the results of the normal- and long-day tests. Theoretically, the net superiority in height shown by ramets of those clones grown in the long-day environment may be attributable to the combined influence of two causes: (1) the longer *season* of growth; and (2) the longer *daily* light period. Although the tests were not designed to analyze quantitative growth differences, the available data suggest that the longer daily light period did not materially contribute to the net seasonal height increment of plants grown in the long day. The superiority in the height of plants given the long-day treatment appears, thus, to have resulted solely from their longer growing season.

Other Environmental Factors Influencing Time of Height Growth Cessation

In general, little disparity was noted in the time of height growth cessation among ramets of the various clones when grown under the influence of the same day-length regime during the same or even succeeding seasons

(TABLE 1). Most minor fluctuations (1 to 10 days) may doubtless be attributed to inaccuracies inherent in the measurement technique employed. Others, demonstrating fluctuations of a higher order, such as the 21-day difference in date of height growth cessation of clone 1324 (TABLE 1) as recorded at Weston and the Arnold Arboretum in 1951, suggest the modifying influence of other factors on the photoperiodic reaction.

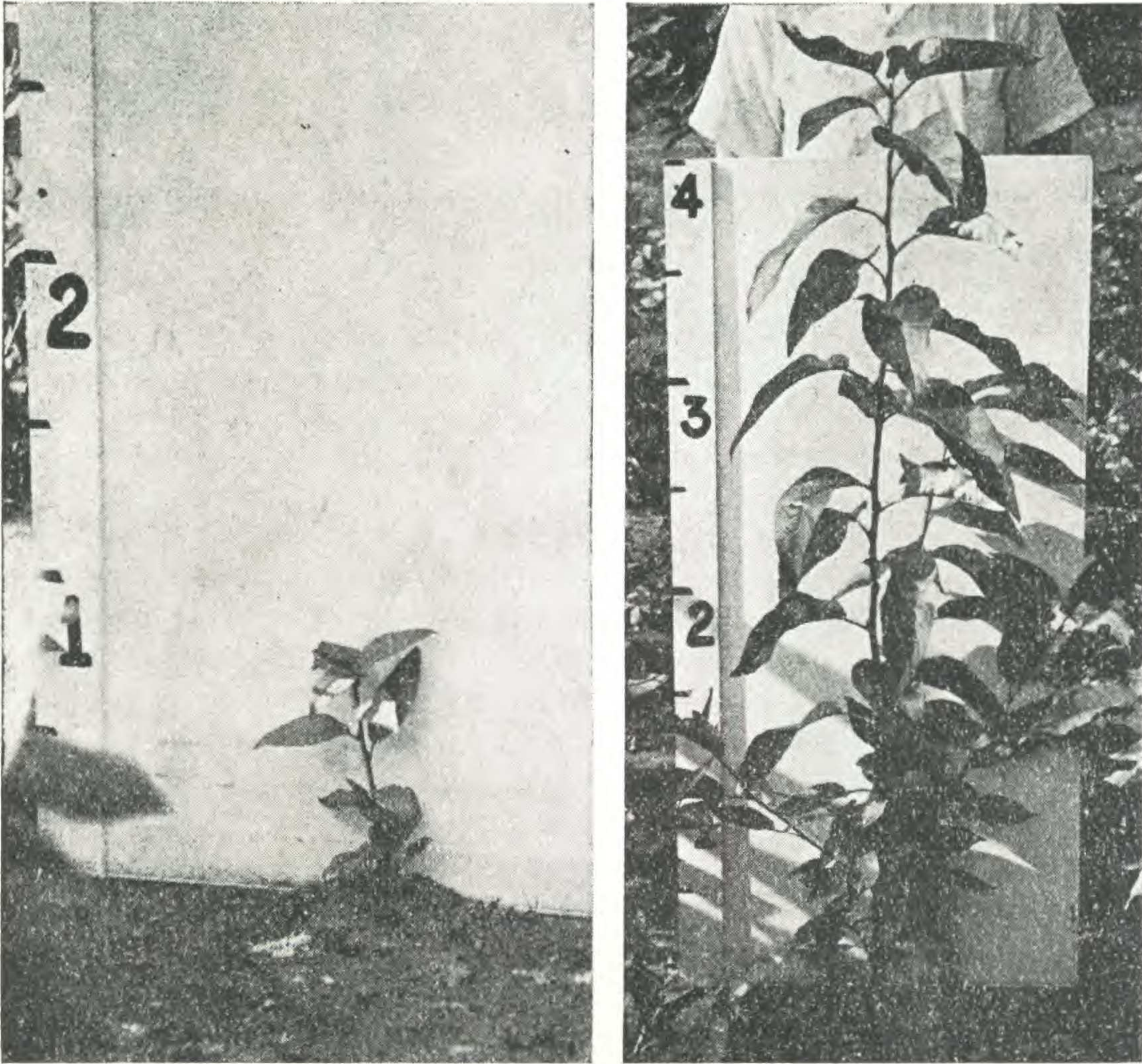


FIG. 7. Diversity in phenotype demonstrated by ramets of *P. trichocarpa* clone No. 984 when grown in the normal day-length regime of Boston (*left*); and in an artificially created long-day regime approximating that of its native Alaskan habitat (*right*). Height growth ceased in the ramet exposed to Boston day length on June 20, 1951; that exposed to the long-day regime stopped growth 60 days later (August 19, 1951). Scale is in feet.

That other environmental factors should serve to modify the photoperiodic response is by no means unusual. Among the factors most suspect is temperature. Garner and Allard (3) observed modification in the photoperiodic requirement for soy beans when grown in different temperatures, and similar reports have been made by other workers (Roberts and Struckmeyer, 17; and Parker and Borthwick, 16). Since most differences in time of height growth cessation between ramets of the same clone

grown at Weston and the Arnold Arboretum were due to earlier cessation of growth at Weston, the uniformly lower temperatures of that locality may have been responsible. (Differences in the natural day length of the two localities is negligible, since they are separated by only ca. 2 minutes of latitude.)

On the basis of experiments currently in progress, there is evidence that ramets of a clone grown in sod may be induced to stop height growth at an earlier date than those grown in cleanly cultivated soil.

There is some indication that excesses of available nitrogen in the soil (Kramer, 8) delay the onset of dormancy in apple trees, and this factor may thus influence time of height growth cessation.

In addition to the above factors, the quite empirical conclusion may be drawn that an apparent intraclonal diversity in physiological functions may frequently develop among ramets of a clone. Such differences appear to be associated with mechanical injury or attack by disease or insects.

ROLE OF THE PHOTOPERIODIC RESPONSE IN THE ANNUAL GROWTH CYCLE OF *POPULUS* SPECIES

Break of Dormancy and Early Seasonal Growth

Although light exerts a profound influence on growth activity during a large portion of the growing season in *Populus*, neither light nor its periodicity appears to be directly concerned in the break of dormancy.

In the propagation area at Weston, marked intra- and interspecific differences in time of leaf flushing are annually observable in early spring; but preliminary results of forcing studies made in 1950, 1951, and 1952 indicated that such differences reflect a diversity in response to prevailing temperatures, apparently acting quite independently of the light environment. In order to test more adequately for a possible light influence on dormancy break, ramets of various clones and sibs of several progenies representing species in all sections of *Populus* were grown in continuous light, natural day, and continuous darkness for a period of ca. three months in the late winter and early spring of 1953. The three compartments were maintained at as uniform a temperature as the facilities available permitted (ca. 70° F.).

Significantly, break of dormancy was negotiated without apparent incident by all plants in the dark compartment.¹ Within those clones and seedling families which broke dormancy early, little disparity (0–2 days) in date of dormancy break between compartments was noted. Within the late-breaking clones and seedling families, there were, however, marked divergencies (3–9 days); but there was no indication that complete ab-

¹ So-called "break of dormancy" in these studies was based on observed separation of bud scales. As *Populus* buds swell, the imbricate bud scales separate, revealing the transparent portion of the underlying scale. Examination of the plants in the dark compartment was effected by use of weak yellow light which, in addition to the green portion of the spectrum, is reported to be photoperiodically ineffective, at least in the flowering response (Miller, 11).

sence of light was more inhibiting to the break of dormancy than continuous light.

Date of appearance of the first unrolled leaf was also recorded in these studies. In most cases the flattening process was not complete in the plants subjected to the dark treatment.

Subsequent growth of the plants in darkness gave rise to the typical morphological modifications associated with etiolation, i.e., reduction in leaf size, marked elongation of the shoot with the development of a hook at the end, inhibited diametral growth, and loss of the erect habit (FIG. 8).



FIG. 8. 1-year seedlings of *P. trichocarpa* grown for 5 weeks in normal day (left); continuous light (center); and continuous darkness (right). All plants were dormant at the start of the experiment and all broke dormancy 8 to 10 days later.

Results of these studies appear to confirm the conclusion that the photoperiod is ineffective in the break of dormancy or early growth in length of *Populus*. Later, however, a stage in the annual growth cycle is reached when the day length must be greater than a certain minimum in order for height growth to continue. As has been demonstrated, high latitude clones of *P. trichocarpa*, when grown in the natural-day regime at the latitude of Boston, cease height growth on or about the time of the summer solstice. If, however, the photoperiod is lengthened by the addition of artificial illumination, they continue to grow, ceasing only when the day length again falls below the critical minimum. The role of the photoperiod in the annual growth cycle of *Populus* thus appears to be primarily effective in the timing of physiological processes concerned in the onset of dormancy.

Diametral Growth Cessation

On the basis of weekly recordings of height and diametral increment made on representatives of various *Populus* species in the plantations at Weston and elsewhere during the 1952 season, it is clear that diametral growth is always terminated after height growth ceases. Interclonal differences in the length of time between height and diametral growth cessation ranged from ca. 10 to 30 days; but there appears to be little evidence from these data to suggest that diametral growth cessation is independently controlled by the photoperiod. A more likely explanation seems to be that cessation of growth in diameter is simply one of the final, and perhaps more or less automatic, steps in the dormancy process.

INHERITANCE OF THE PHOTOPERIODIC RESPONSE

The broad and continuous range in time of height growth cessation which characterizes the behavior of the various ecotypes in these studies, suggests that a large number of genes are involved in the photoperiodic reaction. Further indications of multiple factor inheritance are contained in the records on height growth cessation for the offspring and parents of a north-south cross included in the 1951 studies. Under the influence of either the normal- or long-day regime, the progeny ceased height growth at a time intermediate to that of their parents (Table 2).

TABLE 2

NORTH-SOUTH CROSS
DATE OF HEIGHT GROWTH CESSATION FOR PARENTS (183A × 118) AND
PROGENY (1599 AND 1600)

Clone No.	Lat. of origin	Date of Height Growth Cessation, 1951	
		Normal-day Plot	Long-day Plot
183A	58-30	8/10	9/15
118	46-50	9/12	10/3
1599		8/25	9/21
1600		8/24	9/20

PRACTICAL AND THEORETICAL SIGNIFICANCE OF THE PHOTOPERIODIC GROWTH RESPONSE

Seed Source

Although it would be unwise on the basis of our present limited knowledge to extend the results of these studies to all ligneous species, several practical generalizations concerning the photoperiodic response in trees and its importance in seed source problems may be noted.

- (1) The utilization of seed from northern long-day races for planting in

southern latitudes of long growing season will result in early seasonal growth cessation and consequent dwarfing. Such seed sources should obviously be avoided for the establishment of forest plantations from which maximum production of wood or fiber is desired. On the other hand, such seed sources might prove suitable for the establishment of protection forests in short growing season habitats at high elevations in southern latitudes. The typically small annual increment of northern races when grown in a short-day environment might even make them suitable for special horticultural uses.

(2) Seed derived from ecotypes native of the short growing season, high-altitude habitats of mountainous areas in the low latitudes may be expected to react in a manner similar to northern long-day types and should therefore be avoided as seed sources for forest plantations at the same or more southern latitudes. Such sources of seed may, however, prove highly desirable for introduction into certain long-day environments in northern latitudes having suitably long growing seasons. Support for this generalization is attested by the long history of successful North American tree introductions into the maritime countries of Europe. Conversely, movement of long-day races of native European species into the United States has not met with notable success.

(3) Ecotypes native of long growing season habitats in any particular latitude should be avoided as seed sources for short season habitats at the same latitude because of their susceptibility to early autumn frost damage. For the same reason, such seed sources cannot be successfully moved northward into a long-day environment.

The problem of selecting suitable seed sources of any species for introduction into another environment must obviously take into consideration numerous other environmental factors and genetic characteristics. The above recommendations may be found useful, therefore, only to the extent that they may contribute to limiting the field of search for desirable genotypes. Final decisions on adaptability of the proposed introduction to the new habitat must be based on the observed interaction that results between the introduced genotype and all the factors of its new environment.

Breeding

Because of its fundamental role in the vegetative growth cycle, the photoperiodic response should obviously be a matter of primary concern to the tree breeder. As a means of increasing the net yields of wood or fiber, gene combinations nicely adapted for full utilization of the growing season in a particular habitat, may well prove to be quite as promising as a search for heterotic hybrids.

In view of the probably high genetic diversity of the photoperiodic response in wild tree populations occupying a wide diversity of habitats, initial concern should be directed to the selection of suitable parental materials. This is especially true in F_1 breeding programs and may, to a large extent, explain the unsatisfactory results that have been obtained

by various workers through the selection of parental stocks based on their taxonomic identity and availability, rather than their genetic quality.

Since the photoperiodic response appears to be controlled by a large number of factors, the production of a wide-ranging, transgressive series of photoperiodic types may be expected in F_2 populations. Theoretically, by the initial use of parental ecotypes which give reactions approaching the extremes in day-length response, an F_2 will result which may be expected to contain gene combinations adaptable to almost any growing season length at any latitude.

SUMMARY

For the purpose of studying ecotypic variation in *Populus*, a living collection representative of the ranges of various species in this genus was undertaken in 1947 by the Maria Moors Cabot Foundation for Botanical Research. The studies here reported are concerned primarily with the influence of the photoperiod on time of height growth cessation as observed in the various test areas located in the vicinity of Boston, Massachusetts.

Marked variation in the time that height growth stopped was observed between clonal lines of single species when grown in the same day-length regime and otherwise uniform environment. Analysis of these data revealed that the time of height growth cessation was inversely correlated with the latitude of origin of each clone. Among clones native of uniform day-length zones, the time at which height growth ceased was directly correlated with the length of the frost-free season prevailing in the native habitat of each clone. On the basis of these observations, the conclusion is made that adaptation of *Populus* species to various habitats differing in length of frost-free season is effected by a genetic mechanism which controls the duration of their seasonal period of growth. The photoperiod, which is the only factor of the environment with a uniform seasonal variation that is constant from year to year, functions as the timing device for this mechanism.

Modifications in time of height growth cessation were effected by exposing ramets of various clones to artificially lengthened or shortened photoperiods in otherwise uniform environments. The time of height growth cessation was thus demonstrated to be the result of an interaction between the individual's genotype and the photoperiod. Also observed were other intraclonal modifications in time of height growth cessation that could not be attributed to photoperiodic response. Differences in temperature, available nitrogen, intensity of cultivation, and various other factors are believed to exert a modifying influence on the time that height growth ceases.

Hybrids between clones of northern and southern origin gave a photoperiodic response intermediate to the responses of the parents. These results, and the widely varying photoperiodic responses shown by the various ecotypes used in these studies, indicate that the number of genes involved in the photoperiodic reaction is large.

Experiments on the break of dormancy in the spring indicated that temperature rather than photoperiod is the major factor controlling the initiation of new growth after the period of winter dormancy.

Several practical generalizations concerning the photoperiodic response in trees and its importance in seed source problems and in breeding are noted.

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